A global meta-analysis of the relative extent of intraspecific trait variation in plant communities

Siefert, Andrew ; Violle, Cyrille ; Chalmandrier, Loïc ; Albert, Cécile H ; Taudiere, Adrien ; Fajardo, Alex ; Aarssen, Lonnie W ; Baraloto, Christopher ; Carlucci, Marcos B ; Cianciaruso, Marcus V ; de L. Dantas, Vinícius ; de Bello, Francesco ; Duarte, Leandro D S ; Fonseca, Carlos R ; Freschet, Grégoire T ; Gaucherand, Stéphanie ; Gross, Nicolas ; Hikosaka, Kouki ; Jackson, Benjamin ; Jung, Vincent ; Kamiyama, Chiho ; Katabuchi, Masatoshi ; Kembel, Steven W ; Kichenin, Emilie ; Kraft, Nathan J B ; Lagerström, Anna ; Bagousse-Pinguet, Yoann Le ; Li, Yuanzhi ; Mason, Norman ; Messier, Julie ; Nakashizuka, Tohru ; Overton, Jacob McC ; Peltzer, Duane A ; Pérez-Ramos, I M ; Pillar, Valério D ; Prentice, Honor C ; Richardson, Sarah ; Sasaki, Takehiro ; Schamp, Brandon S ; Schöb, Christian ; Shipley, Bill ; Sundqvist, Maja ; Sykes, Martin T ; Vandewalle, Marie ; Wardle, David A

Abstract: Recent studies have shown that accounting for intraspecific trait variation (ITV) may better address major questions in community ecology. However, a general picture of the relative extent of ITV compared to interspecific trait variation in plant communities is still missing. Here, we conducted a meta-analysis of the relative extent of ITV within and among plant communities worldwide, using a data set encompassing 629 communities (plots) and 36 functional traits. Overall, ITV accounted for 25% of the total trait variation within communities and 32% of the total trait variation among communities on average. The relative extent of ITV tended to be greater for whole-plant (e.g. plant height) vs. organ-level traits and for leaf chemical (e.g. leaf N and P concentration) vs. leaf morphological (e.g. leaf area and thickness) traits. The relative amount of ITV decreased with increasing species richness and spatial extent, but did not vary with plant growth form or climate. These results highlight global patterns in the relative importance of ITV in plant communities, providing practical guidelines for when researchers should include ITV in trait-based community and ecosystem studies.

DOI: https://doi.org/10.1111/ele.12508

Sasaki, Takehiro; Schamp, Brandon S; Schöb, Christian; Shipley, Bill; Sundqvist, Maja; Sykes, Martin T; Vandewalle, Marie; Wardle, David A (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters, 18(12):1406-1419.
DOI: https://doi.org/10.1111/ele.12508

A global meta-analysis of the relative extent of intraspecific trait variation in plant communities

Andrew Siefert[1], Cyrille Violle[2], Loïc Chalmandrier[3,4], Cécile H. Albert[5], Adrien Taudiere[2], Alex Fajardo[6], Lonnie W. Aarssen[7], Christopher Baraloto[8], Marcos B. Carlucci[9,10,11], Marcus V. Cianciaruso[12], Vinícius de L. Dantas[13], Francesco de Bello[14,15], Leandro D. S. Duarte[9], Carlos R. Fonseca[16], Grégoire T. Freschet[2,17], Stéphanie Gaucherand[18], Nicolas Gross[19,20], Kouki Hikosaka[21], Benjamin Jackson[22], Vincent Jung[23], Chiho Kamiyama[24], Masatoshi Katabuchi[25], Steven W. Kembel[26], Emilie Kichenin[17], Nathan J. B. Kraft[27], Anna Lagerström[17], Yoann Le Bagousse-Pinguet[15], Yuanzhi Li[28], Norman Mason[29], Julie Messier[30], Tohru Nakashizuka[31], Jacob McC. Overton[29], Duane Peltzer[32], I. M. Pérez-Ramos[33], Valério D. Pillar[9,34], Honor C. Prentice[35], Sarah Richardson[32], Takehiro Sasaki[36], Brandon S. Schamp[37], Christian Schöb[38], Bill Shipley[28], Maja Sundqvist[39,40], Martin T. Sykes[41], Marie Vandewalle[41], David A. Wardle[17]

[1] Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

[2] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE - 34293 Montpellier, France

[3] Université Grenoble Alpes, LECA, F-38000 Grenoble, France

[4] CNRS, LECA, F-3800 Grenoble, France

[5] Aix Marseille Université, CNRS, IRD, Avignon Université, IMBE, 13397, Marseille, France

[6] Centro de Investigación en Ecosistemas de la Patagonia (CIEP) Conicyt–Regional R10C1003, Universidad Austral de Chile, Camino Baguales s/n, Coyhaique 5951601, Chile

[7] Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada

[8] INRA, UMR Ecologie des Forêts de Guyane, BP 709, 97387 Kourou Cedex, France

[9] Programa de Pós Graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS 91501-970, Brazil

[10] CAPES Foundation, Ministry of Education of Brazil, Brasília, DF 70040-020, Brazil

[11] Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás, 74690-900, Goiânia, Goiás, Brazil

[12] Departamento de Ecologia, Universidade Federal de Goiás, 74690-900, Goiânia, Goiás, Brazil

[13] Department of Plant Biology, University of Campinas, 13083-970, Campinas, São Paulo, Brazil

[14] Institute of Botany, Czech Academy of Sciences, CZ-379 82, Třeboň, Czech Republic

[15] Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

[16] Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN, 59092-350, Brazil

[17] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umea 901 83, Sweden

[18] IRSTEA, Unité de Recherche sur les Ecosystèmes Montagnards, BP 76, 38402, St-Martin d'Hères, cedex, France

[19] INRA, USC1339 Chizé (CEBC), F-79360, Villiers en Bois, France

[20] Centre d'étude biologique de Chizé, CNRS - Université La Rochelle (UMR 7372), F-79360, Villiers en Bois, France

[21] Graduate School of Life Sciences, Tohoku University, Aoba, Sendai 980-8578, Japan

[22] Centre for Ecology and Hydrology, Library Avenue, Bailrigg, LA14AP, Lancaster, UK

[23] CNRS UMR 6553, ECOBIO, Université de Rennes 1, 35042 Rennes, France

[24] Institute for the Advanced Study of Sustainability, United Nations University, 5-53-70 Jingumae, Shibuya 150-8925, Japan

[25] Department of Biology, University of Florida, P.O. Box 118525, Gainesville, FL, 32611, USA

[26] Département des sciences biologiques, Université du Québec à Montréal, Montréal, Québec, H3C3P8 Canada

[27] Department of Biology, University of Maryland, College Park, MD, 20742, USA

[28] Département de biologie, Université de Sherbrooke, Sherbrooke (Qc) J1K 2R1, Canada

[29] Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

[30] Ecology and Evolutionary Biology, University of Arizona, 1041 E. Lowell Street, Tucson, AZ, 85721, USA

[31] Graduate School of Life Sciences, Tohoku University, Aoba, Sendai 980-8578, Japan

[32] Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

[33] Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Sevilla 41080, Spain

[34] Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[35] Department of Biology, Lund University, Sölvegatan 37, SE-223 62 Lund, Sweden

[36] Graduate School of Frontier Sciences, University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba, 277-8563, Japan

[37] Department of Biology, Algoma University, Sault Ste. Marie, Ontario, P6A 2G4, Canada

[38] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zürich, Switzerland

[39] Department of Ecology and Environmental Science, Umeå University, SE901 87 Umeå, Sweden

[40] Center for Macroecology, Evolution and Climate, The Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen, Denmark

[41] Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

Running title: Intraspecific variation in plant communities

Keywords: community ecology, functional diversity, interspecific variation, intraspecific variability, leaf trait, plant functional trait, trait-based ecology

Type of article: Reviews & Syntheses

Number of words in abstract: 179
Number of words in main text: 6967
Number of references: 77
Number of figures: 5
Number of tables: 0
Number of text boxes: 1 (348 words)

Corresponding author: Andrew Siefert
Mailing address: Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA
E-mail: asiefert@ucdavis.edu
Phone: 814-490-8935

Statement of authorship: AS conceived of and designed the study. All authors collected and analyzed data. AS and LC conducted the meta-analysis. AS, CV, LC, CA, and AT wrote the first draft of the manuscript, and all authors contributed to revisions.

Abstract

Recent studies have shown that accounting for intraspecific trait variation (ITV) may better address major questions in community ecology. However, a general picture of the relative extent of ITV compared to interspecific trait variation in plant communities is still missing. Here, we conducted a meta-analysis of the relative extent of ITV within and among plant communities worldwide, using a dataset encompassing 629 communities (plots) and 36 functional traits. Overall, ITV accounted for 25% of the total trait variation within communities and 32% of the total trait variation among communities on average. The relative extent of ITV tended to be greater for whole-plant (e.g. plant height) versus organ-level traits and for leaf chemical (e.g. leaf N and P concentration) versus leaf morphological (e.g. leaf area and thickness) traits. The relative amount of ITV decreased with increasing species richness and spatial extent, but did not vary with plant growth form or climate. These results highlight global patterns in the relative importance of ITV in plant communities, providing practical guidelines for when researchers should include ITV in trait-based community and ecosystem studies.

Introduction

In recent decades, an explosion of research on functional diversity, which measures the values of functional traits and their variation within and among communities, has shed new light on community assembly and ecosystem processes (Weiher & Keddy 1995; Diaz & Cabido 2001; Hooper *et al.* 2005; McGill *et al.* 2006; Kraft *et al.* 2008). By working with functional traits, researchers seek generalizable predictions across organizational and spatial scales (Adler *et al.* 2013). The dominant theories and approaches in trait-based community ecology have focused largely on trait differences among species (McGill *et al*. 2006), but there has recently been renewed interest in the role of intraspecific trait variation (ITV) (Bolnick *et al.* 2011; Violle *et al.* 2012). This interest is grounded in the observation that functional traits vary at the individual level, and this variation influences the interactions among organisms and between organisms and their environment that ultimately drive the assembly and functioning of communities (Bolnick *et al.* 2003; Vellend & Geber 2005). Integrating ITV in community ecology thus has the potential to strengthen understanding of processes operating at the community level and ecosystem levels.

Recent studies have demonstrated that accounting for ITV may be critical for answering key questions and making predictions about plant community assembly and ecosystem functioning (Violle *et al.* 2012). Plants often display strong intraspecific variation in functional traits, reflecting both heritable genetic variation and phenotypic plasticity, and this variation influences plant responses to abiotic filters and biotic interactions (Fridley *et al.* 2007; Fridley & Grime 2010), as well as plant effects on ecosystem processes (Crustinger *et al.* 2006; Hughes *et al.* 2008). Recent studies have found that consideration of ITV improves the ability of trait-based analyses to make inferences about local community assembly processes (Jung et al. 2010; Paine et al. 2011; Siefert 2012a). Accounting for ITV has also been shown to improve predictions of

157 outcomes of species interactions (Kraft *et al.* 2014), community responses to spatial and
158 temporal environmental gradients (Lepš *et al.* 2011; Kichenin *et al.* 2013; Jung *et al.* 2014), and
159 ecosystem processes such as productivity and nutrient cycling (Breza *et al.* 2012).

160 Despite the predictive power that may come from considering ITV in plant community
161 studies, a practical limitation is the difficulty of measuring trait values on a large number of
162 individuals per species, particularly in species-rich communities (Baraloto *et al.* 2010). When
163 and how ITV should be incorporated in trait-based ecology studies has thus emerged as an urgent
164 question (Albert *et al.* 2011). Although many factors go into answering this question, a basic
165 consideration is the relative amount of intraspecific compared to interspecific trait variation in
166 the communities being studied. If ITV is large compared to interspecific variation, it is likely to
167 have important ecological consequences and should not be ignored out of hand. Recently,
168 empirical studies have quantified the relative amount of ITV compared to interspecific variation
169 for various plant functional traits and communities (e.g. Jung *et al.* 2010; Messier *et al.* 2010;
170 Lepš *et al.* 2011; Auger & Shipley 2012). This work has shown that the extent of ITV within and
171 among plant communities is often substantial—sometimes similar to or greater than interspecific
172 variation—but highly context-dependent, varying strongly among traits and communities. An
173 improved understanding of the context-dependence of ITV in plant communities is necessary for
174 integrating ITV in trait-based ecology and for understanding its role in ecological processes
175 acting at the community scale and beyond (Albert *et al.* 2011). To address this need, we
176 conducted a global-scale meta-analysis to determine the relative extent of ITV compared to
177 interspecific variation in plant communities and to identify general trends in how ITV varies
178 among traits and study systems.

179 The first aim of our meta-analysis was to make generalizations about how ITV varies
180 among functional traits and broad trait categories. Previous studies examining inter- and
181 intraspecific trait variation in plant communities have found that the relative extent of ITV varies
182 strongly among traits. For example, Hulshof & Swenson (2010), partitioning variation in four
183 leaf traits in a tropical forest in Costa Rica, found that ITV ranged from 36-83% of total trait
184 variance. Our global meta-analysis approach allowed us to identify traits that consistently display
185 high ITV across systems and to test general hypotheses about how ITV varies among trait
186 categories. First, we tested whether the relative extent of ITV differs between traits measured at
187 the whole-plant level (e.g. plant height, plant architecture) and at the organ level (leaves, stems,
188 and roots). Based on plant optimization models (Marks 2007), we expected that traits measured
189 at higher levels of plant integration (i.e. whole-plant traits) should be highly sensitive to the
190 environment and thus display high ITV as a result of local genetic adaptation and phenotypic
191 plasticity. In contrast, we expected organ-level traits to be more strongly conserved and thus vary
192 mostly at the interspecific level (Marks 2007). Then, focusing on leaf traits, we tested whether
193 the relative extent of ITV differed between traits related to leaf chemical composition—e.g.
194 elemental concentrations and ratios—and traits related to leaf morphology—e.g. leaf area, leaf
195 thickness, specific leaf area (SLA), leaf dry matter content (LDMC). Comparative studies have
196 found that leaf nutrient concentrations are highly labile within species, displaying strong plastic
197 responses to resource availability, whereas leaf morphology tends to be more stable (Rozendaal
198 *et al.* 2006; Kazakou *et al.* 2014). We therefore expected leaf chemical traits to show higher
199 relative ITV at the community level than leaf morphological traits.
200 The second aim of this meta-analysis was to examine how ITV varies among
201 communities differing in terms of the dominant growth form, species richness, and climate. First,

202 we asked whether the relative extent of ITV differs between communities consisting of woody
203 versus herbaceous plants. We may expect long-lived (i.e. woody) species to have high
204 ontogenetic variation and express strong phenotypic plasticity to face environmental hazards
205 over their lifetimes, leading to high ITV (Sultan 1987; Borges 2009). Conversely, species with
206 long tissue lifespan may have higher costs or limits to plasticity, and we might thus expect them
207 to express less ITV than fast-growing, ruderal (i.e. herbaceous) species (Maire *et al.* 2013).
208 Second, we tested whether the relative extent of ITV varies with community species richness.
209 Previous work suggests that ITV should be most important in species-poor communities (e.g.
210 MacArthur 1984; Antonovics 1992; Whitham *et al.* 2006), and niche theory predicts that the
211 relative extent of ITV should decrease with increasing species richness (Violle *et al.* 2012).
212 However, few studies have empirically examined this relationship in plant communities, and
213 these have produced conflicting results (Hulshof *et al.* 2013; Le Bagousse-Pinguet *et al.* 2014).
214 Finally, we tested whether the relative extent of ITV varies with climate (temperature and
215 precipitation) on a global scale. Previous research suggests that phenotypic plasticity may be
216 constrained in stressful environments (Valladares *et al.* 2007). If this is true, we expect the
217 relative extent of ITV to decrease with increasing climatic stress (i.e. decreasing temperature and
218 precipitation). Alternatively, several hypotheses predict that unfavorable conditions increase the
219 expression of genetic variability in traits, leading to the opposite pattern (Hoffmann & Merilä
220 1999). Community-level ITV has rarely been measured across broad climatic gradients (but see
221 Hulshof *et al.* 2013), so these hypotheses remain largely untested.
222 Third, we examined how the relative extent of ITV depends on the spatial scale (grain
223 and extent) of observation across studies. Interspecific and intraspecific trait variation are both
224 expected to increase with spatial extent as broader environmental gradients are encountered,

leading to turnover of species and genotypes as well as plastic trait responses (Albert *et al.* 2011; Auger & Shipley 2013). However, ITV must saturate at some scale once the entire potential genetic and environmental variation of species is reached. Therefore, the relative contribution of ITV to trait variation among communities is expected to decrease with increasing spatial extent from local to regional and global scales (Albert *et al.* 2011) or with increasing distance along environmental gradients (Auger & Shipley 2013). At the community level, the relationship between spatial grain (plot or sampling unit size) and the relative extent of ITV within communities is more difficult to predict. For example, this relationship may depend on the scale of environmental heterogeneity relative to the size of individual plants, and thus the potential for individuals to express genetic and plastic trait differences across different environments.

In assessing the extent and role of ITV in plant communities, it is important to recognize that ITV arises from multiple mechanisms, including heritable genetic variation, phenotypic plasticity, and ontogenetic variation, and these mechanisms will differentially affect whole-plant versus organ-specific traits. While specific sources of variation may be of interest for investigating particular ecological or evolutionary questions, all sources contribute to the trait variation observed in natural communities and potentially influence community assembly and ecosystem processes. Understanding the extent and consequences of ITV at the community level, even if its underlying mechanisms are unknown, is therefore an important step for trait-based ecology (Violle *et al.* 2012). Moreover, partitioning the sources of ITV—for example, using classical methods from quantitative genetics (Vellend *et al.* 2014)—may not be feasible at the community level except in systems dominated by one or few species. In our meta-analysis, we therefore considered all potential sources of ITV and did not attempt to distinguish them. ITV may also be measured at different levels of organization, including within-individual (e.g.

248 variation among leaves within a plant), among-individual, and among-population or site. Here,
249 we focused on ITV at two levels of organization. Specifically, we aimed to quantify 1) the
250 relative contribution of among-individual ITV to the total trait variation within plant
251 communities (within-community analysis), and 2) the relative contribution of among-population
252 ITV to the total variation in mean trait values among plant communities (among-community
253 analysis).

254 Overall, we quantified the relative extent of ITV within and among plant communities
255 using a dataset consisting of 44 studies, encompassing 629 plant communities (plots) worldwide
256 and 36 plant functional traits. Using these data, we conducted a meta-analysis to address two
257 main questions: 1) how does the relative extent of ITV vary among plant functional traits and
258 among broad trait categories? 2) Can variation in the relative extent of ITV among studies be
259 explained by basic properties of the studied communities, including plant growth form, species
260 richness, climate, and spatial scale? By addressing these questions, we provide the broadest and
261 most thorough assessment to date of the importance of ITV to community-level functional
262 diversity. Our findings suggest practical guidelines for when ITV is likely to be substantial in
263 plant communities and therefore important to include in trait-based community and ecosystem
264 studies.

265

266 **Methods**

267 **A global dataset to assess ITV in plant communities**

268 To conduct our meta-analysis, we assembled data from published and unpublished studies by the
269 authors that measured intraspecific trait variation within and among terrestrial, vascular plant
270 communities. Criteria for including a study in the within-community analysis were 1) species

composition data including relative abundance for at least one community (defined here as a single plot or sampling unit); and 2) trait measurements on at least five individuals (or all individuals if total was fewer than five) per species per community. Criteria for including a study in the among-community analysis were 1) species composition data including relative abundance for three or more communities; and 2) trait measurements on at least one individual per species per sampled community. For both within- and among-community analyses, we only included studies that measured traits of species that together made up at least 80% of total community abundance (variously measured as cover, density, biomass, or frequency) as recommended in previous studies (Pakeman & Quested 2007). Following typical methods in plant community ecology, many studies focused on a single vegetation layer (e.g. trees or herbs), even if multiple layers were present in the study area. We included these studies in the analysis, acknowledging that they may include only a subset of the vascular vegetation in a given area.

Following the trait definition of Violle *et al.* (2007), we included in our dataset morphological and physiological features of plants measurable at the individual level. Further, we sought to include traits known to be related to some aspect of plant functioning, i.e. functional traits. As the goal of this study is to give a general picture of the relative extent of ITV in plant communities, and given the diversity of ecological questions that functional traits can be used to address, we preferred to be inclusive with our selection of traits. Characters such as plant height and canopy dimensions measured at the individual level, for instance, may be viewed as measures of performance rather than indicators of plant strategy in the context of community assembly studies. However, individual variation in such characters still contributes to the standing phenotypic variation within and among communities, with potential consequences for coexistence, ecosystem functioning, and other processes. We conducted analyses with plant

294 height either included or excluded; as both approaches produced similar results, we present only
295 results with height included for completeness.
296 We classified the traits in our dataset by organ (whole-plant, leaf, stem, or root), and leaf
297 traits were in turn categorized as morphological (i.e. related to overall leaf size, shape, density, or
298 mechanical properties) or chemical (i.e. describing leaf chemical composition). To simplify the
299 analysis and allow for generalization, we combined data for closely related traits (e.g. vegetative
300 and reproductive height). A summary of traits included in our dataset and description of their
301 ecological significance are found in Tables S1 and S2 in the Supporting Information.
302 For each study, we collected metadata including geographic coordinates, spatial grain
303 (area of single community, i.e. sampling unit, in m^2), spatial extent (maximum geographic
304 distance between communities in km), ecosystem type (tropical or temperate), growth form
305 (woody, herbaceous, or both), and alpha and gamma species richness (mean number of species
306 within communities and total number of species across all communities in a study, respectively).
307 For each study, we extracted mean annual temperature (MAT) and mean annual precipitation
308 (MAP) values from WorldClim (http://www.worldclim.org). We also obtained information on
309 sampling design and effort, including the number of communities, percent of total species
310 richness and total community abundance sampled, and number of individuals and populations
311 sampled per species. Studies varied in their methods of selecting individuals and leaves within
312 individuals for trait measurement. Most studies selected individuals randomly, only avoiding
313 damaged or unhealthy individuals, but some studies only included individuals from particular
314 life stages or size classes (e.g. adult trees or saplings), thus reducing ITV association with
315 ontogeny. For leaf traits, some studies selected leaves randomly within each individual, but most
316 studies—following standard trait protocols (Perez-Harguindeguy *et al.* 2013)—selected only

young, fully-expanded, outer canopy leaves, thus reducing ITV associated with light environment and leaf age. We included studies with both random and non-random selection of individuals and leaves in our meta-analysis, acknowledging that this may contribute to unexplained variation in ITV among studies and overall underestimation of ITV.

Our final dataset consisted of 171 study-trait combinations (cases), representing 33 studies and 30 unique traits, with data suitable for the within-community analysis; and 214 trait-study combinations from 37 studies, representing 36 traits, with data suitable for the among-community analysis (see Tables S1, S3). The studies covered a broad geographic range (Fig. 1) and included all major global biomes except deserts. For both datasets, studies measuring woody species were more common than studies of herbaceous or combined woody and herbaceous species. Among plant organs, leaf traits were best represented, followed by whole-plant, stem, and root traits. Leaf morphological traits were better represented than leaf chemical traits. The individual traits with the greatest number of observations were specific leaf area (SLA), plant height, leaf dry matter content (LDMC), leaf thickness, bark thickness, wood density, leaf length, and leaf area (see Table S1).

Data analysis

We used the framework developed by Lepš *et al.* (2011) and de Bello *et al.* (2011) to evaluate the relative contribution of intraspecific trait variation to total within-community (*wITV*) and among-community (*aITV*) trait variance for each trait and study (see Box 1 for details). Our *wITV* metric represents the proportion of total within-community trait variance attributable to ITV. The *aITV* metric represents the relative contribution of intraspecific trait variation versus species turnover to the total among-community variance, with positive values indicating a greater contribution of ITV and negative values indicating a greater contribution of species

turnover. Differences in *wITV* and *aITV* among traits and studies could be driven by differences in the absolute extent of interspecific or intraspecific variation, or a combination of the two. Disentangling these sources is an interesting research question (see e.g. Hulshof *et al.* 2013; Le Bagousse-Pinguet *et al.* 2014), but here we focused on the relative rather than absolute extent of ITV, because it allows comparison of multiple traits measured in different units or on different scales, for which comparison of raw variance values would be difficult or impossible.

We evaluated the factors influencing the relative extent of ITV within (*wITV*) and among communities (*aITV*) using linear mixed models and an information-theoretic approach (Burnham & Anderson 2002). For each response variable (*wITV* and *aITV*), we performed separate analyses on all traits together (including only traits measured in at least two studies), leaf traits only, and the two most commonly sampled individual traits in our dataset, SLA and plant height. We also performed separate analyses on the dataset divided by growth form (woody or herbaceous) and biome (temperate or tropical).

For analyses of all traits and leaf traits, we developed a set of linear mixed models that included trait and study as random effects and all possible combinations of the following fixed effects: mean annual temperature (MAT), mean annual precipitation (MAP), alpha species richness (*wITV* analysis only), gamma species richness (*aITV* analysis only), spatial grain, spatial extent (*aITV* analysis only), growth form, organ (whole-plant, leaf, stem, or root; only for analysis of all traits) and leaf trait category (morphological or chemical; leaf trait analyses only). For analyses of single traits (SLA and plant height), we used simple linear regressions with species richness, grain, extent, and growth form as fixed effects. Species richness and spatial grain and extent were log-transformed to reduce skewness. We excluded models that contained highly correlated ($|r| > 0.5$) predictor variables. The combinations of variables excluded varied

among analyses, but in most cases temperature, precipitation, and species richness were positively correlated, and thus no more than one of these predictors was included in each model. Additionally, spatial extent and grain were positively correlated, so no more than one of them was included in each model when analyzing *aITV*.

The models were ranked according to the corrected Akaike information criterion (AICc) and their relative support was evaluated with the AICc weight (Burnham & Anderson 2002). We retained a confidence set of models with cumulated AICc weight of 0.95 (Johnson & Omland 2004). The relative importance of each fixed effect in the confidence set was calculated as the sum of the Akaike weights over all of the models in which it appeared. We further calculated model averaged estimates of the fixed effects over the confidence set of models (Burnham & Anderson 2002).

Finally, to test whether variation in the relative extent of ITV among traits was consistent across organizational scales (within- and among-community), we examined the relationship between mean *wITV* and *aITV* across traits. We calculated the average *wITV* and *aITV* across studies for each trait, using only studies that measured both *wITV* and *aITV* for a given trait. We tested whether mean *wITV* and *aITV* were correlated using reduced major axis regression and a permutation test. All analyses were conducted using R version 3.0.2 (R Core Development Team 2012) using packages lme4 (Bates *et al.* 2013) and MuMIn (Bartoń 2013).

Results

Relative extent of ITV within communities

Across all studies and traits, ITV accounted for on average 25% of the total within-community trait variance, with interspecific variance accounting for the remainder (intercept of random

386 effects only model for *wITV* = 0.25; 95% confidence interval = 0.19-0.31). There was
387 considerable variation in the relative extent of ITV among traits and studies, with values ranging
388 from 2 to 67% (Fig. 2a; Table S1). Of the most commonly measured traits, ITV tended to be
389 relatively high for SLA, plant height, leaf N, and LDMC (median *wITV* = 25-30%; Fig. 2a), and
390 lower for wood density and leaf area, leaf thickness, and leaf length (median *wITV* < 20%; Fig.
391 2a). There was no effect of any variable relating to sample size or sampling effort on *wITV*.
392 Results of linear mixed model analysis of all traits showed that the relative extent of ITV
393 within communities was negatively related to species richness and greater for whole-plant traits
394 than for leaf traits (Fig. 3a; Appendix S1). The analysis of leaf traits showed that *wITV* was
395 marginally greater for chemical compared to morphological traits (Fig. 3b). For SLA, *wITV*
396 decreased marginally with increasing MAT (Fig. 3c). For plant height, *wITV* was negatively
397 related to species richness and decreased marginally with increasing mean annual temperature
398 and precipitation (Fig. 3d).
399 The relative extent of ITV within communities did not differ between studies measuring
400 woody versus herbaceous species (relative importance of growth form = 0.10; Fig. 3), but the
401 effects of species richness, organ, and leaf trait category were all stronger for woody
402 communities (see Appendix S2). There was also a marginal negative effect of MAP on *wITV* for
403 woody but not for herbaceous communities (Appendix S2). Temperate and tropical communities
404 did not differ in *wITV* (relative importance of biome = 0), but the effects of species richness and
405 organ were stronger for temperate communities (see Appendix S2). In addition, *wITV* decreased
406 with increasing spatial grain in temperate but not in tropical communities (Appendix S2).
407 **Relative extent of ITV among communities**

Across all studies and traits, ITV accounted for 32% of the total trait variation among communities on average, whereas species turnover accounted for 64% (intercept of random effects model for *aITV* = -0.94; 95% confidence interval = -1.64 to -0.24). For individual traits, there were cases in which the average contribution of ITV was greater than (*aITV* > 0, e.g. leaf N:P; Fig. 2b; Table S1), similar to (*aITV* = 0; e.g. SLA, LDMC, leaf C:N), or much less than that of species turnover (*aITV* < 0; e.g. leaf size traits). Of the commonly measured traits, the relative contribution of ITV was greatest for plant height, bark thickness, and LDMC and least for leaf area, length, and thickness (Fig. 2b; Table S1). The covariation between ITV and species turnover was highly variable but was most often weakly positive (median = 7.7%), indicating that traits tended to vary in the same direction due to ITV and species turnover. Overall, *aITV* was not influenced by any variable related to sample size or sampling effort.

The relative extent of ITV among communities was negatively related to spatial grain and extent (Fig. 4a; Appendix S3). The analysis of leaf traits showed that *aITV* was greater for chemical than morphological traits (Fig. 4b). For SLA, *aITV* decreased marginally with increasing grain, extent, and precipitation and was lower for studies that included both woody and herbaceous growth forms than for studies with only woody or herbaceous species (Fig. 4c). For plant height, *aITV* was marginally negatively related to gamma species richness and spatial extent (Fig. 4d).

Although growth form (woody versus herbaceous) was not an important factor in explaining *aITV* when looking at all community types together (relative importance of growth form = 0.06), we found differences in the effects of predictors when analyzing woody and herbaceous communities separately (see Appendix S3). In particular, there was a strong negative effect of precipitation and positive effect of gamma species richness on *aITV* for herbaceous but

not for woody communities (Appendix S4). Similarly, there was no overall difference in *aITV* between temperate and tropical communities (relative importance of biome = 0), but the effects of spatial extent, growth form, and leaf trait category were much stronger for tropical communities (see Appendix S4). In addition, there was a negative effect of temperature on *aITV* in tropical but not temperate communities (Appendix S4).

Relationship between within- and among-community ITV across traits

Mean *wITV* and *aITV* were positively correlated across traits ($R^2 = 0.42$; $P < 0.01$), indicating that traits with a high relative extent of ITV within communities also had high ITV among communities (Fig. 5). Most traits fell near the overall regression line, but some traits (e.g. leaf thickness) were well above the line, indicating relatively higher ITV among than within communities. Conversely, some traits (e.g. leaf carbon concentration and lateral spread) fell well below the regression line, indicating relatively higher ITV within than among communities.

Discussion

Our global meta-analysis revealed that ITV often contributes substantially to the total trait variation within and among plant communities but is typically less than interspecific variation. On average, ITV accounted for 25% of total within-community trait variance and 32% of total among-community variance in mean trait values. Below, we discuss general trends in the context-dependence of the relative extent of ITV in plant communities and the implications of these findings for trait-based ecology.

Variation in relative extent of ITV among functional traits

The relative extent of ITV varied strongly among the traits examined in this study, and we identified several general patterns with respect to broad trait categories. First, leaf chemical traits

454 tended to have greater ITV within and among communities compared to leaf morphological
455 traits. This result is in line with previous studies finding high ITV in leaf chemical traits. For
456 example, Kazakou *et al*. (2014), examining leaf trait variation in a common garden experiment
457 and Mediterranean old-fields, found that ITV accounted for >60% of total variation in leaf N, P,
458 and C concentrations. Storage of carbon and nutrients by plants, which depends on element
459 availability in the environment, may explain the high intraspecific variability in leaf chemical
460 composition (Chapin *et al.* 1990), but heritable genetic variability may also contribute to
461 differences among individuals and populations. Our finding that ITV is an important source of
462 variation in leaf chemical traits across community types and biomes worldwide has strong
463 implications for studies of nutrient cycling and decomposition. Leaf chemical traits of plant
464 communities are known to exert a strong influence on nutrient cycling and decomposition rates
465 (Quested *et al.* 2007; Cornwell *et al.* 2008), and intraspecific variability in these traits is likely to
466 play a role in driving spatial and temporal variation in these processes.
467 We also found strong differences in the relative extent of ITV for leaf traits related to
468 different aspects of plant function. ITV within communities was relatively high (25% or more of
469 total community trait variation) for both chemical and morphological traits linked to the leaf
470 economics spectrum (e.g. leaf N and P, SLA, LDMC). This is consistent with previous studies
471 finding extensive ITV in leaf economic traits arising from plastic responses to light, nutrients,
472 and other environmental factors (Meziane & Shipley 1999; Rozendaal *et al.* 2006), as well as
473 genetic variability and ontogenetic variation (Scheepens *et al.* 2010; Vasseur *et al.* 2012; Mason
474 *et al.* 2013). Our finding that leaf economic traits consistently display high ITV within and
475 among communities globally has important implications for trait-based ecology. Leaf economic
476 traits represent a primary axis of functional variation in plants worldwide and are linked to a

proposed universal 'fast-slow' plant economics spectrum that may help explain individual plant strategies, community assembly, and ecosystem functioning (Reich 2014). The high intraspecific variability in leaf economic traits suggests that ITV may play an important role in community- and ecosystem-level processes and deserves increased consideration in future studies. In contrast to leaf economic traits, ITV was low for traits related to leaf size (area, length, width, thickness), which are typically considered independent of the leaf economics spectrum but have been linked with adaptation to broad climatic gradients (Craine *et al.* 2012). Previous studies have found that leaf size traits have limited plasticity and low ITV relative to the large interspecific variation among co-occurring species (Rozendaal et al. 2006). Our findings suggest that species mean trait values are likely to capture the majority of leaf size variation within and among most plant communities worldwide.

Finally, we found that within-community ITV tended to be greater for whole-plant traits than for organ-level traits. This result is consistent with predictions of plant optimization models (Marks 2007), which show that variation in whole-plant traits is primarily driven by environment, whereas variation in organ-level traits is more tightly constrained by phylogeny. Since plants grow by iterating terminal modules (organs), and since the rate of accumulation of such modules is partly determined by resource supplies from the environment, ITV is expected to be higher in traits involving several modules (i.e. whole-plant traits) than in traits involving a single terminal module. We were only able to include two whole-plant traits, plant height and lateral spread, in our analysis, and studies measuring additional whole-plant traits are needed to provide more general tests of these predictions. Maximum plant height is considered an important plant strategy indicator that is linked to light acquisition and competitive ability (Westoby 1998; Violle *et al.* 2009). The large ITV in plant height in our meta-analysis may

reflect genetic variability in maximum height, but also likely includes large environmental and ontogenetic components, which are less clearly related to plant strategy and community assembly.

Variation in relative extent of ITV with community properties

The relative extent of ITV within communities decreased with increasing species richness across all traits and studies. Post-hoc analysis of our dataset showed that for most traits, this relationship was primarily due to an increase in interspecific variance (and thus total community trait variance) with increasing richness, while ITV remained relatively constant. Few previous studies have examined relationships between species richness and community-level trait variation, particularly ITV, and these have produced conflicting results. For example, Lamanna *et al.* (2014), examining tree assemblages in the New World, found a positive relationship between species richness and total community trait space, which is consistent with our results. Hulshof *et al.* (2013), working in woody plant communities along elevational and latitudinal gradients, found a negative relationship between species richness and the ratio of intraspecific to interspecific variance in SLA, suggesting that as species richness increased, species' niches became more tightly packed in trait space, relative to the total space occupied by the community. Similarly, our finding that the relative extent of ITV decreases with increasing species richness indicates that individual species tend to occupy smaller proportions of the total community trait space in more species-rich communities, consistent with niche theory (MacArthur & Levins 1967; Violle *et al.* 2012). In contrast, Le Bagousse-Pinguet *et al.* (2014), working in experimental grassland communities, found that ITV and the ratio of ITV to total community trait variance were positively related to species richness, suggesting greater trait overlap between species in more species-rich communities.

Our findings highlight the importance of accounting for ITV in species-poor communities, where ITV is more likely to account for a large proportion of total community functional diversity (Fajardo & Piper 2011). Whether ITV should be included in studies of species-rich communities will likely depend on the goals of the study, as well as practical considerations. It is important to recognize that while our results show that the relative extent of ITV tends to decrease with increasing species richness, the absolute extent of ITV does not. In addition, previous work cautions against the use of species mean trait values for estimating community trait means and variances, even in species-rich communities (Baraloto *et al.* 2010).

The relative extent of ITV varied surprisingly little with climate or growth form, suggesting that the patterns we observed are generally consistent across global biomes and plant community types. There was a weak tendency for the relative extent of ITV to increase with decreasing mean annual temperature and precipitation, consistent with the hypothesis that expression of genetic and environmental trait variation is increased in stressful conditions (Hoffmann & Merilä 1999). This result should be interpreted with caution, however, as temperature, precipitation, and species richness were positively correlated in our dataset, making it difficult to separate the effects of specific factors. Moreover, while we used mean annual temperature and precipitation as predictors to capture global-scale variation in climate, our dataset encompassed multiple, complex environmental gradients, making broad generalization difficult. Future studies examining patterns of trait variation along specific environmental gradients predicted to influence plant community assembly, or experimentally manipulating these factors, are needed to test hypotheses about the relationship between inter- and intraspecific functional variation and abiotic stress.

545 The relative extent of ITV also did not vary consistently between studies measuring
546 woody versus herbaceous species. ITV was hypothesized either to be higher in longer-lived,
547 woody plants as a result of developmental and plastic variation in response to temporal
548 environmental variation (Sultan 1987; Borges 2009), or lower in such plants because longer
549 tissue lifespan may impose higher costs or limits to plasticity (Maire *et al.* 2013). Our analysis
550 did not support either hypothesis, possibly because both processes were acting and neutralized
551 each other. Confounding differences between woody and herbaceous study systems in our
552 dataset may also have made it difficult to detect general patterns. Comparing the relative extent
553 of ITV in woody versus herbaceous species within specific community types may provide a
554 stronger test of these hypotheses. We note that, while there was no difference in the relative
555 extent of ITV between studies measuring only woody or herbaceous species, ITV tended to be
556 lower in studies that included both growth forms. This result is not surprising, given the large
557 interspecific variation in many traits between woody and herbaceous species, and it suggests that
558 the relative importance of ITV decreases as the taxonomic or functional scope of a study
559 increases.

560 **Relationship between ITV and spatial scale**

561 Consistent with our prediction, the contribution of ITV (relative to that of species turnover) to
562 among-community trait variation tended to decrease with increasing spatial extent—i.e., the
563 maximum distance between sites in a study. This pattern is likely to be driven by the increasing
564 breadth of environmental gradients encountered at larger spatial extents. Increasing
565 environmental gradient breadth leads to increased species turnover and thus interspecific trait
566 variation, but at some point probably exhausts the potential genetic and plastic trait variability of
567 individual species (Albert *et al.* 2011; Auger & Shipley 2013). Previous studies have shown that

ITV contributes strongly to changes in community mean trait values along relatively narrow, local-scale environmental gradients (e.g. Jung *et al.* 2010; Pérez-Ramos *et al.* 2012), with species turnover becoming more important as the breadth of environmental gradients increases (Siefert *et al.* 2014). Our findings support the use of species mean trait values in functional biogeography studies (Violle *et al.* 2014, 2015) examining relationships between environmental factors and community trait distributions at broad spatial scales, although ITV could still be important in systems dominated by relatively few widely-distributed species (Fajardo & Piper 2011).

Spatial grain, defined here as the area of individual sampling units or communities, had an inconsistent effect on the relative amount of ITV within communities. In herbaceous communities, there was a negative relationship between grain and the relative extent of ITV, while in woody communities, the relationship was positive. These contrasting results may relate to differences in the scale on which plants of different size perceive environmental variation. Previous studies have shown that a large proportion of the ITV of herbaceous plant species occurs at relatively fine spatial scales (Albert et al. 2010; Siefert 2012b), indicating strong intraspecific trait responses to fine-scale environmental heterogeneity and saturation of ITV with increasing scale. In contrast, larger, woody plants acquire resources across wider areas, integrating over such fine-scale variation (Hutchings *et al.* 2003), so that small plots contain little effective environmental variation and thus low ITV of woody species. With increasing grain size, plots contain more effective environmental variation from the plant perspective, leading to increased ITV (relative to interspecific trait variation). Overall, these results lead us to hypothesize that the relative extent of ITV should be maximized at intermediate grain sizes, with the location of the peak depending on the size of the organisms and scale of environmental heterogeneity in a given study.

591

592

593 **Relationship between within- and among-community ITV across traits**

594 In general, we found that the relative extent of ITV within and among communities was
595 positively correlated across traits. In other words, traits that had relatively high ITV within
596 communities also had high ITV among communities, indicating consistency across levels of
597 organization addressed in plant community ecology studies. The few exceptions to this trend
598 may represent traits for which ITV is primarily driven by factors operating at either within- or
599 among-community scales. For example, lateral spread had the highest relative within-community
600 ITV of any trait in our study, but lower-than-average relative ITV among communities. This may
601 suggest strong intraspecific responses to competition and other biotic interactions occurring
602 within communities, but weak responses to among-community environmental gradients. In
603 contrast, leaf thickness displayed moderate relative ITV among communities but extremely low
604 relative ITV within communities. This is consistent with relatively strong intraspecific responses
605 of leaf thickness to broad-scale climatic gradients, but weak responses to fine-scale biotic
606 interactions.

607 **Limitations**

608 We were able to conduct the broadest assessment to date of the relative extent of ITV in plant
609 communities, but several aspects of our dataset may limit the generality of our findings. First, we
610 had little or no data on several types of potentially important functional traits, including root,
611 reproductive, and phenological traits. Second, several globally important community types (e.g.
612 deserts) and geographic regions (e.g. Africa) were missing or underrepresented. Third, studies
613 varied in the method of selecting individuals and leaves for trait measurement. Notably, many

studies selected individuals non-randomly (e.g. mature, healthy-looking individuals growing in full sun) according to established trait sampling protocols (Perez-Harguindeguy *et al.* 2013), which likely resulted in underestimation of ITV. Additional work is needed to better understand the influence of sampling effort and design on the quantification of the absolute and relative amount of ITV within and among communities, but the optimum methods will likely depend on the goals and questions of specific studies.

We also recognize, as previously mentioned, that our analysis was unable to distinguish between ITV arising from phenotypic plasticity and heritable genetic differences. We are not aware of any study that has quantified the contributions of these sources to overall trait variation at the community level. Doing so would require a tremendous amount of effort and may only be feasible for communities dominated by one or few species (Grassein *et al.* 2010). We speculate that plastic trait variation is likely to be larger than intraspecific genetic variation for most traits and communities, given the low heritability typically observed for plant functional traits in field conditions (Geber & Griffen 2003), although exceptions certainly exist (see e.g. Donovan *et al.* 2010) . The consequences of different sources of ITV for community and ecosystem-level processes are little understood. The relative extent of plastic vs. genetic trait variation may have important consequences for community responses to environmental change (Lavergne *et al.* 2010), since plastic trait responses are expected to be rapid but limited in scope, whereas adaptive evolutionary responses may be broader in scope but proceed more slowly (Gienapp *et al.* 2008). While quantification of the relative amount of ITV in communities as done here is a first necessary step for community ecology, disentangling the extent and consequences of plastic and genetic trait variation at the community and ecosystem levels certainly remains a major challenge for future researchers.

637 **Recommendations for including ITV in trait-based studies**

638 The results of our meta-analysis suggest some general guidelines for when ITV is likely to be
639 substantial and therefore important to consider in plant community and ecosystem studies (Albert
640 *et al.* 2011). First, ITV consistently accounts for a significant proportion of the total within- and
641 among-community trait variation in whole-plant traits and leaf economic traits including leaf
642 chemical traits, SLA, and LDMC; we therefore recommend that researchers consider ITV in
643 studies measuring these traits. As many of these traits have been strongly implicated in
644 community assembly and ecosystem functioning, integrating ITV in future studies should lead to
645 improved understanding of these processes. Second, the decrease in the relative importance of
646 ITV with increasing spatial extent suggests that it is most relevant to consider ITV in studies
647 conducted on local scales and short environmental gradients. Conversely, functional
648 biogeography studies may provide robust broad-scale interpretations without accounting for ITV
649 (Violle *et al.* 2014). Third, the increase in the relative extent of ITV with decreasing species
650 richness emphasizes the need to account for ITV in studies of species-poor communities, in
651 which individual species may fill a large proportion of the total community trait space. Having
652 made these recommendations, we stress that the relative magnitude of ITV is not the only factor
653 determining whether and to what degree ITV will influence ecological processes. Even when
654 ITV is relatively low, it can have large effects at the community level (e.g. Jung *et al*. 2010).
655 Nevertheless, knowing the relative extent of ITV for a given trait and study system is an
656 important step for designing trait-based plant ecology studies, and this information may also
657 provide input for simulations to test the importance of ITV for specific ecological questions
658 (Albert *et al.* 2011).

In conclusion, this study provides the first global assessment of the relative extent of ITV in plant communities. Our results confirm that ITV often accounts for a significant proportion of the total functional diversity within and among communities and demonstrate that the relative extent of ITV varies predictably among traits and with species richness and spatial scale. Beyond quantifying the extent of ITV, the next step for trait-based plant community ecology is to more systematically test how this variation influences community and ecosystem processes and dynamics (Enquist *et al.* 2015).

Acknowledgements

We thank Mark Westoby, Ian Wright, and three anonymous reviewers for providing valuable comments on an earlier version of the manuscript. AS was supported by the National Science Foundation Graduate Research Fellowship (DGE-1247399) and NSF grant DEB-03089. CV was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Program (DiversiTraits project, no. 221060) and by the European Research Council (ERC) Starting Grant Project "Ecophysiological and biophysical constraints on domestication in crop plants" (Grant ERC-StG-2014-639706-CONSTRAINTS). LC received funding from the European Research Council under the 7th European Community Framework Program FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO). Financial support to AF came from the Chilean Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT) project No. 1120171. LWA and BSS were supported by Discovery Grants from the Natural Science and Engineering Research Council of Canada. LDSD and VDP received fellowships from the Brazilian Research Council (grants 303534/2012-5 and 306573/2009-1). CS was supported by the Swiss National Science Foundation (PA00P3_136474 and PZ00P3_148261).

MVC, LDSD, VDP, and CRF were supported by CAPES-Brazil (grant BEX 7913/13-3) and CNPq-Brazil (grants 479083/2008-8, 141451/2011-4, 306573/2009-1, 303534/2012-5, and 303714/2010-7). MK received support from the JSPS as a Postdoctoral Fellow for Research Abroad. VLD was supported by Sao Paulo Research Foundation (process: 2014/06453-0). DAP, SJR, and NWHM were supported by the New Zealand Ministry of Business, Innovation and Employment core funding to Crown Research Institutes and the Ministry for the Environment. YLBP was supported by the project Postdoc USB (reg.no. CZ.1.07/2.3.00/30.0006) realized through EU Education for Competitiveness Operational Programme and received funding from the European Social Fund and Czech State Budget. The Forest Dynamics Plot of Yasuni National Park has been made possible through the generous support of the Pontifical Catholic University of Ecuador, the government of Ecuador, the Andrew W. Mellon Foundation, the Smithsonian Tropical Research Institute, and the University of Aarhus of Denmark.

References

1.
Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013). Trait-based tests of coexistence mechanisms. *Ecol. Lett.*, 16, 1294–1306.
2.
Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.*, 13, 217–225.
3.
Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., *et al.* (2010). Intraspecific functional variability: extent, structure and sources of variation. *J. Ecol.*, 98, 604–613.
4.
Antonovics, J. (1992). Toward community genetics. In: *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics* (eds. Fritz, R.S. & Simms, E.L.). University of Chicago Press, USA, pp. 426–449.
5.
Auger, S. & Shipley, B. (2013). Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *J. Veg. Sci.*, 24, 419–428.
6.

715 Baraloto, C., Paine, C.E.T., Patiño, S., Bonal, D., Hérault, B. & Chave, J. (2010). Functional trait
716 variation and sampling strategies in species-rich plant communities. *Funct. Ecol.*, 24, 208–216.
717 7.
718 Bartoń, K.A. (2013). MuMIn: multi-model inference. R package version 1.9.13.
719 8.
720 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2013). lme4: mixed-effects model using Eigen
721 and S4. R package version 1.0-4.
722 9.
723 De Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., *et al.* (2011).
724 Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods Ecol.*
725 *Evol.*, 2, 163–174.
726 10.
727 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011).
728 Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26, 183–192.
729 11.
730 Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., *et al.* (2003).
731 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*,
732 161, 1–28.
733 12.
734 Borges, R.M. (2009). Phenotypic plasticity and longevity in plants and animals: cause and
735 effect? *J. Biosci.*, 34, 605–611.
736 13.
737 Breza, L.C., Souza, L., Sanders, N.J. & Classen, A.T. (2012). Within and between population
738 variation in plant traits predicts ecosystem functions associated with a dominant plant species.
739 *Ecol. Evol.*, 2, 1151–1161.
740 14.
741 Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical*
742 *information-theoretic approach*. Springer, New York, USA.
743 15.
744 Chapin, F.I., Schulze, E. & Mooney, H. (1990). The ecology and economics of storage in plants.
745 *Annu. Rev. Ecol. Syst.*, 21, 423–447.
746 16.
747 Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., *et*
748 *al.* (2008). Plant species traits are the predominant control on litter decomposition rates within
749 biomes worldwide. *Ecol. Lett.*, 11, 1065–1071.
750 17.
751 Craine, J.M., Ocheltree, T.W., Nippert, J.B., Towne, E.G., Skibbe, A.M., Kembel, S.W., *et al.*
752 (2012). Global diversity of drought tolerance and grassland climate-change resilience. *Nat. Clim.*
753 *Change*, 3, 63–67.
754 18.
755 Crustinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., Sandrews, N.J., *et al.*
756 (2006). Plant genotypic diversity predicts community structure and governs an ecosystem
757 process. *Science*, 313, 966–8.
758 19.
759 Donovan, L.A., Maherali, H., Caruso, C.M., Huber, H. & de Kroon, H. (2010). The evolution of
760 the worldwide leaf economics spectrum. *Trends Ecol. Evol.*, 26, 88–95.

20.
Díaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
21.
Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., *et al.* (2015). Scaling from traits to ecosystem: developing a general Trait Driver Theory via integrating trait-based and metabolic scaling theories. *Adv. Ecol. Res.*, 52, 169-199.
22.
Fajardo, A. & Piper, F.I. (2011). Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. *New Phytol.*, 189, 259–271.
23.
Fridley, J.D. & Grime, J.P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91, 2272–83.
24.
Fridley, J.D., Grime, J.P. & Bilton, M. (2007). Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *J. Ecol.*, 95, 908–915.
25.
Geber, M.A. & Griffen, L.R. (2003). Inheritance and natural selection on functional traits. *Int. J. Plant Sci.*, 164, S21–S42.
26.
Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. & Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.*, 17, 167–178.
27.
Grassein, F., Till-Bottraud, I. & Lavorel, S. (2010). Plant resource-use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. *Ann. Bot.*, 106, 637.
28.
Hoffmann, A.A. & Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.*, 14, 96–101.
29.
Hooper, D., Chapin, F.I., Ewel, J. & Hector, A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
30.
Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.*, 11, 609–23.
31.
Hulshof, C.M. & Swenson, N.G. (2010). Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Funct. Ecol.*, 24, 217–223.
32.
Hulshof, C.M., Violle, C., Spasojevic, M.J., McGill, B., Damschen, E., Harrison, S., *et al.* (2013). Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *J. Veg. Sci.*, 24, 921–931.
33.

807 Hutchings, M.J., John, E.A. & Wijesinghe, D.K. (2003). Toward understanding the
808 consequences of soil heterogeneity for plant populations and communities. *Ecology*, 84, 2322–
809 2334.
810 34.
811 Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol.*
812 *Evol.*, 19, 101–8.
813 35.
814 Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G. & Spiegelberger, T. (2014).
815 Intraspecific trait variability mediates the response of subalpine grassland communities to
816 extreme drought events. *J. Ecol.*, 102, 45–53.
817 36.
818 Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010). Intraspecific variability and
819 trait-based community assembly. *J. Ecol.*, 98, 1134–1140.
820 37.
821 Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., *et al.* (2014). Are trait-
822 based species rankings consistent across data sets and spatial scales? *J. Veg. Sci.*, 25, 235–247.
823 38.
824 Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. (2013). Contrasting
825 effects of plant inter- and intraspecific variation on community-level trait measures along an
826 environmental gradient. *Funct. Ecol.*, 27, 1254–1261.
827 39.
828 Kraft, N.J.B., Crutsinger, G.M., Forrestel, E.J. & Emery, N.C. (2014). Functional trait
829 differences and the outcome of community assembly: an experimental test with vernal pool
830 annual plants. *Oikos*, 1391–1399.
831 40.
832 Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008). Functional traits and niche-based tree
833 community assembly in an Amazonian forest. *Science*, 322, 580–2.
834 41.
835 Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Imova, I., *et al.* (2014).
836 Functional trait space and the latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U.S.A.*, 111,
837 13745-13750.
838 42.
839 Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010). Biodiversity and Climate Change:
840 Integrating Evolutionary and Ecological Responses of Species and Communities. *Annu. Rev.*
841 *Ecol. Evol. Syst.*, 41, 321–350.
842 43.
843 Le Bagousse-Pinguet, Y., de Bello, F., Vandewalle, M., Leps, J. & Sykes, M.T. (2014). Species
844 richness of limestone grasslands increases with trait overlap: evidence from within- and between-
845 species functional diversity partitioning. *J. Ecol.*, 102, 466–474.
846 44.
847 Lepš, J., de Bello, F., Šmilauer, P. & Doležal, J. (2011). Community trait response to
848 environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*,
849 34, 856–863.
850 45.
851 MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of
852 coexisting species. *Am. Nat.*, 101, 377–385.

46.
MacArthur, R.H. (1984). *Geographical ecology: patterns in the distribution of species*. Princeton, NJ, USA.
47.
Maire, V., Soussana, J.-F., Gross, N., Bachelet, B., Pagès, L., Martin, R., *et al.* (2013). Plasticity of plant form and function sustains productivity and dominance along environment and competition gradients. A modeling experiment with Gemini. *Ecol. Model.*, 254, 80–91.
48.
Marks, C.O. (2007). The causes of variation in tree seedling traits: the roles of environmental selection versus chance. *Evolution*, 61, 455–469.
49.
Mason, C.M., McGaughey, S.E. & Donovan, L.A. (2013). Ontogeny strongly and differentially alters leaf economic and other key traits in three diverse *Helianthus* species. *J. Exp. Bot.*, 64, 4089–4099.
50.
McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–85.
51.
Messier, J., McGill, B.J. & Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.*, 13, 838–848.
52.
Meziane, D. & Shipley, B. (1999). Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant Cell Environ.*, 22, 447–459.
53.
Paine, C.E.T., Baraloto, C., Chave, J. & Hérault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos*, 120, 720–727.
54.
Pakeman, R.J. & Quested, H.M. (2007). Sampling plant functional traits: what proportion of the species need to be measured? *Appl. Veg. Sci.*, 10, 91–96.
55.
Pérez-Ramos, I., Roumet, C., Cruz, P., Blanchard, A., Autran, P. & Garnier, E. (2012). Evidence for a "plant community economics spectrum" driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *J. Ecol.*, 100, 1315–1327.
56.
Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., *et al.* (2013). New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.*, 61, 167–234.
57.
Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. (2007). Plant traits relate to whole-community litter quality and decomposition following land use change. *Funct. Ecol.*, 21, 1016–1026.
58
R Core Development Team. (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
59.

899 Reich, P.B. (2014). The world-wide “fast-slow” plant economics spectrum: a traits manifesto. *J.*
900 *Ecol.*, 102, 275–301.
901 60.
902 Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006). Plasticity in leaf traits of 38 tropical
903 tree species in response to light; relationships with light demand and adult stature. *Funct. Ecol.*,
904 20, 207–216.
905 61.
906 Scheepens, J.F., Frei, E.S. & Stöcklin, J. (2010). Genotypic and environmental variation in
907 specific leaf area in a widespread Alpine plant after transplantation to different altitudes.
908 *Oecologia*, 164, 141–50.
909 62.
910 Siefert, A. (2012a). Incorporating intraspecific variation in tests of trait-based community
911 assembly. *Oecologia*, 170, 767–775.
912 63.
913 Siefert, A. (2012b). Spatial patterns of functional divergence in old-field plant communities.
914 *Oikos*, 121, 907–914.
915 64.
916 Siefert, A., Fridley, J.D. & Ritchie, M.E. (2014). Community functional responses to soil and
917 climate at multiple spatial scales: when does intraspecific variation matter? *PLoS One*, 9,
918 e111189.
919 65.
920 Sultan, S.E. (1987). Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.*, 21,
921 127–178.
922 66.
923 Valladares, F., Gialoni, E. & Gómez, J.M. (2007). Ecological limits to phenotypic plasticity.
924 *New Phytol.*, 176, 749–763.
925 67.
926 Vasseur, F., Violle, C., Enquist, B.J., Granier, C. & Vile, D. (2012). A common genetic basis to
927 the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecol. Lett.*, 15, 1149–
928 1157.
929 68.
930 Vellend, M. & Geber, M.A. (2005). Connections between species diversity and genetic diversity.
931 *Ecol. Lett.*, 8, 767–781.
932 69.
933 Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S.W. & Garant, D. (2014). Drawing
934 ecological inferences from coincident patterns of population- and community-level biodiversity.
935 *Mol. Ecol.*, 23, 2890–2901.
936 70.
937 Violle, C., Choler, P., Borgy, B., Garnier, E., Amiaud, B., Debarros, G., *et al.* (2015). Vegetation
938 ecology meets ecosystem science: permanent grasslands as a functional biogeography case study.
939 *Sci. Total Environ.*, in press.
940 71.
941 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., *et al.* (2012). The
942 return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.*, 27,
943 244–252.
944 72.

945 Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A., *et al.* (2009).
946 Competition, traits and resource depletion in plant communities. *Oecologia*, 160, 747–55.
947 73.
948 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.* (2007). Let the
949 concept of trait be functional! *Oikos*, 116, 882–892.
950 74.
951 Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014). The emergence and
952 promise of functional biogeography. *Proc. Natl. Acad. Sci. U.S.A.*, 111, 13690–13696.
953 75.
954 Weiher, E. & Keddy, P.A. (1995). Assembly rules, null models, and trait dispersion: new
955 questions from old patterns. *Oikos*, 74, 159–164.
956 76.
957 Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil*, 199,
958 213–227.
959 77.
960 Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., *et al.*
961 (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat.*
962 *Rev. Genet.*, 7, 510–523.
963

964 **Supporting information**

965 Additional Supporting Information may be downloaded via the online version of this article at
966 Wiley Online Library

967 **Figure Legends**

968

969 **Figure 1.** Locations of studies included in the within-community analysis only (white circles, *n*
970 = 7), among-community analysis only (grey circles, *n* = 11), and both analyses (black circles, *n* =
971 26).
972
973 **Figure 2.** Boxplots showing relative magnitude of intraspecific trait variation (a) within
974 communities (*wITV*) and (b) among communities (*aITV*) for all traits with at least two
975 observations in our dataset. The number of observations (studies) per trait is indicated above the
976 box. Solid horizontal line indicates overall mean value across all traits. Dashed horizontal line
977 indicates equal magnitude of intraspecific and interspecific trait variation (*wITV* = 0.5; *aITV* =
978 0). Values above dashed line indicate larger intraspecific than interspecific variation and vice
979 versa.
980
981 **Figure 3.** Model averaged coefficient estimates and 95% confidence intervals for fixed effects
982 included in confidence set of models explaining relative extent of intraspecific trait variation
983 within communities (*wITV*). Results are shown for analyses of all traits, leaf traits, specific leaf
984 area (SLA), and plant height. Continuous predictors were standardized (mean = 0, sd = 1) to
985 make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights
986 of models in which a given predictor appears. Results are shown only for predictors with RI >
987 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form
988 (herbaceous, woody, or herbaceous and woody); TC: leaf trait category (chemical or
989 morphological).
990 **Figure 4.** Model averaged coefficient estimates and 95% confidence intervals for fixed effects
991 included in confidence set of models explaining relative extent of intraspecific trait variation

among communities (*aITV*). Results are shown for analyses of all traits, leaf traits, specific leaf area (SLA), and plant height. Continuous predictors were standardized (mean = 0, sd = 1) to make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form (herbaceous, woody, or herbaceous and woody); TC: leaf trait category (chemical or morphological).

Figure 5. Relationship between relative magnitude of intraspecific trait variation within (*wITV*) and among (*aITV*) across traits in our dataset. Each point represents the mean *wITV* and *aITV* for a given trait across the studies in which it was measured. Error bars represent standard error. Only cases in which a given trait was measured within- and among-communities in the same study are included in this analysis. Solid line is the ranged major axis regression line. Significance of the relationship was assessed using a permutation test. BT: bark thickness; H: plant height; LA: leaf area; LC: leaf C; LCN: leaf C:N; LDMC: leaf dry matter content; LK: leaf K; LL: leaf length; LP: leaf P; LS: lateral spread; LT: leaf thickness; LW: leaf width; SLA: specific leaf area; WD: wood density.

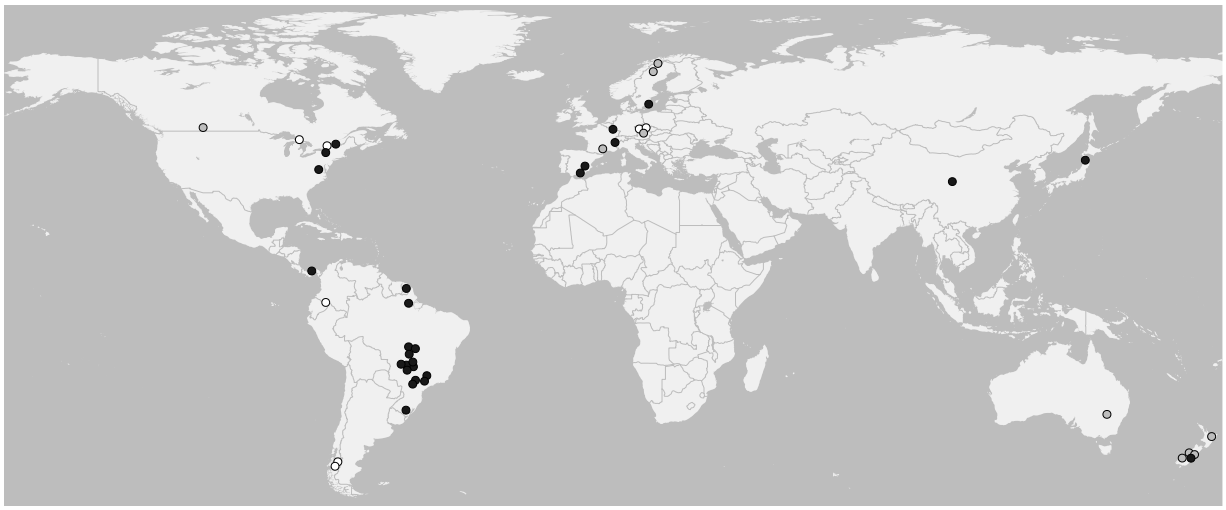

Figure 1

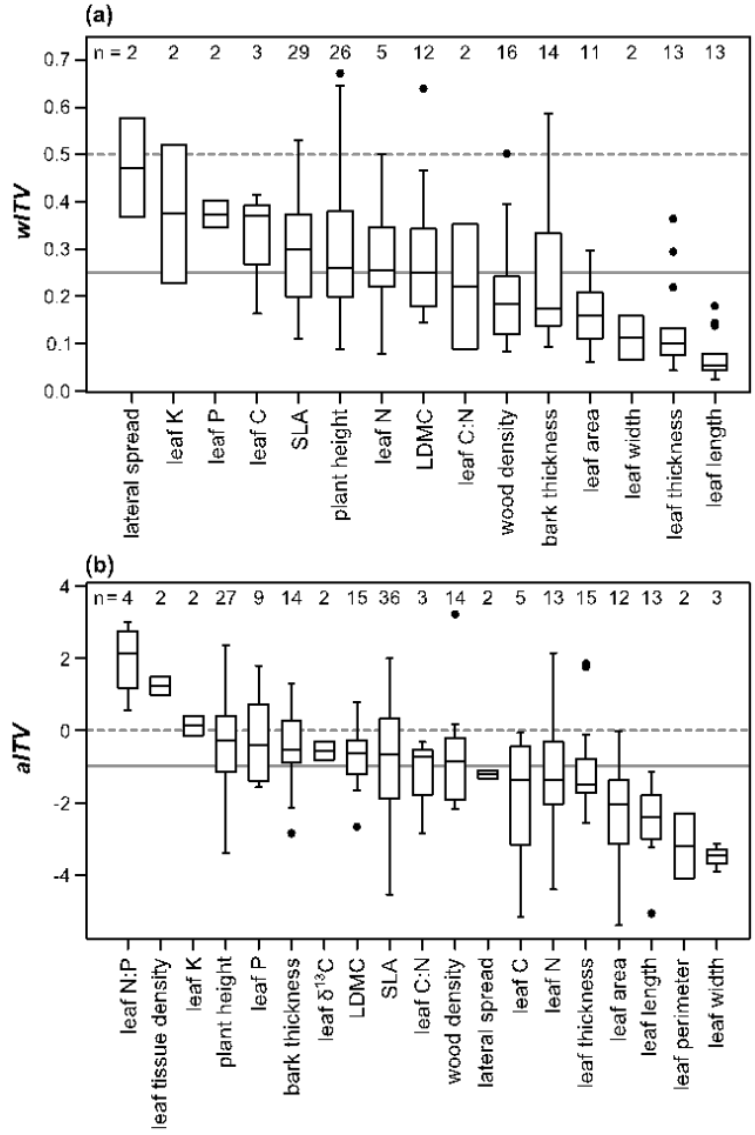
(a)
n = 2 2 2 3 29 26 5 12 2 16 14 11 2 13 13
wITV
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
lateral spread
leaf K
leaf P
leaf C
SLA
plant height
leaf N
LDMC
leaf C:N
wood density
bark thickness
leaf area
leaf width
leaf thickness
leaf length
(b)
n = 4 2 2 27 9 14 2 15 36 3 14 2 5 13 15 12 13 2 3
aITV
4
2
0
-2
-4
leaf N:P
leaf tissue density
leaf K
plant height
leaf P
bark thickness
leaf δ13C
LDMC
SLA
leaf C:N
wood density
lateral spread
leaf C
leaf N
leaf thickness
leaf area
leaf length
leaf perimeter
leaf width

Figure 2

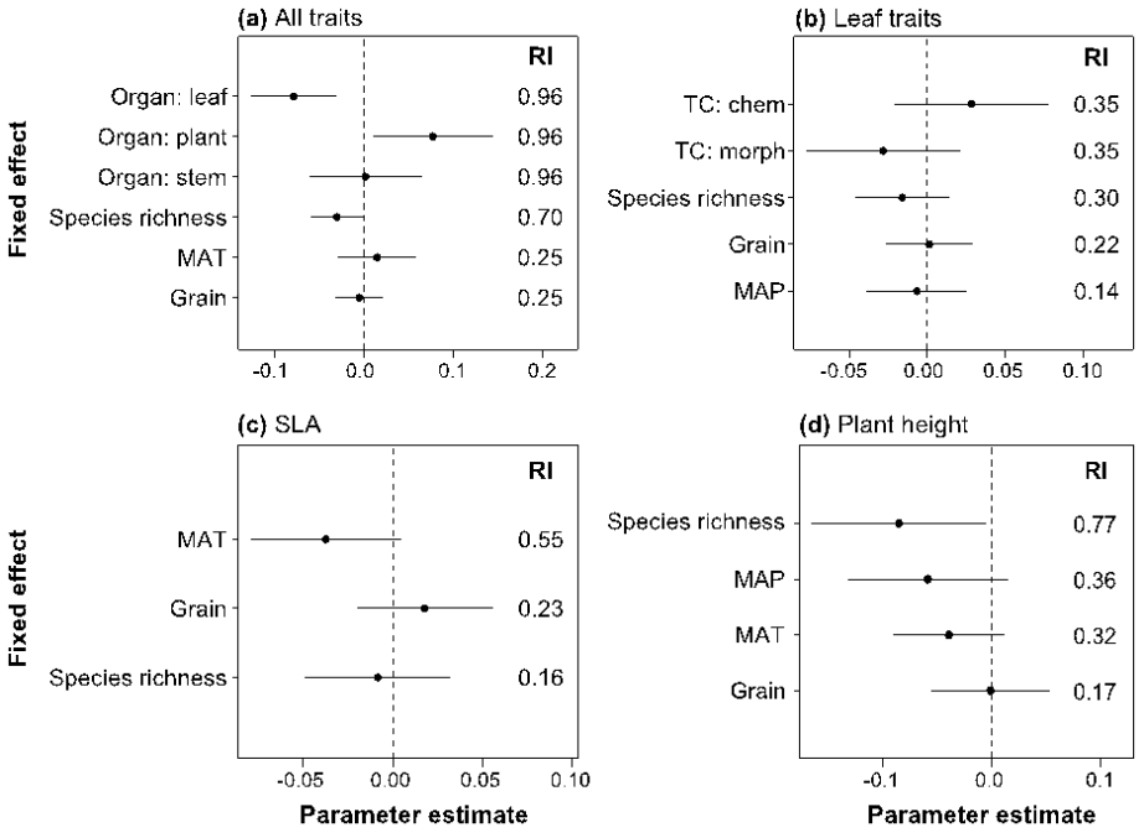
(a) All traits
RI
Organ: leaf
Organ: plant
Organ: stem
Species richness
MAT
Grain
0.96
0.96
0.96
0.70
0.25
0.25
-0.1
0.0
0.1
0.2
(b) Leaf traits
RI
TC: chem
TC: morph
Species richness
Grain
MAP
0.35
0.35
0.30
0.22
0.14
-0.05
0.00
0.05
0.10
(c) SLA
RI
MAT
Grain
Species richness
0.55
0.23
0.16
-0.05
0.00
0.05
0.10
(d) Plant height
RI
Species richness
MAP
MAT
Grain
0.77
0.36
0.32
0.17
-0.1
0.0
0.1
Fixed effect
Fixed effect
Parameter estimate
Parameter estimate

Figure 3

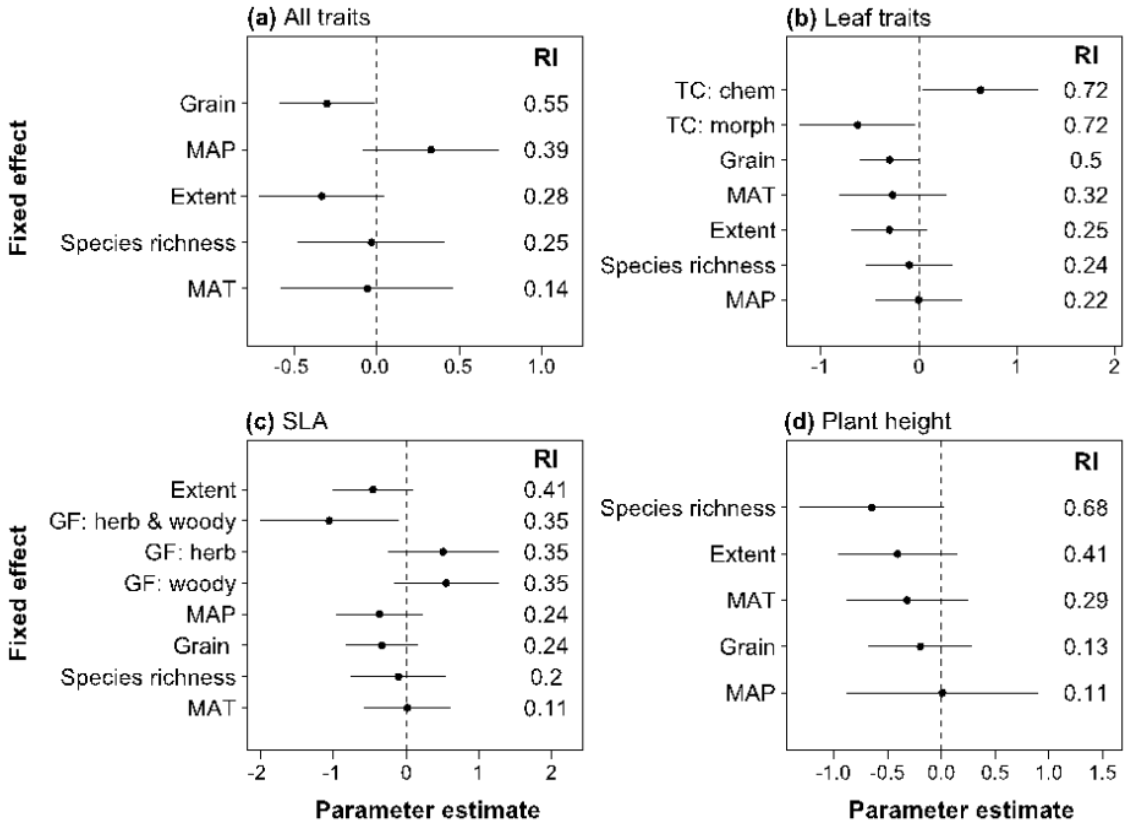
(a) All traits
RI
Grain 0.55
MAP 0.39
Extent 0.28
Species richness 0.25
MAT 0.14
-0.5 0.0 0.5 1.0
(b) Leaf traits
RI
TC: chem 0.72
TC: morph 0.72
Grain 0.5
MAT 0.32
Extent 0.25
Species richness 0.24
MAP 0.22
-1 0 1 2
(c) SLA
RI
Extent 0.41
GF: herb & woody 0.35
GF: herb 0.35
GF: woody 0.35
MAP 0.24
Grain 0.24
Species richness 0.2
MAT 0.11
-2 -1 0 1 2
Parameter estimate
(d) Plant height
RI
Species richness 0.68
Extent 0.41
MAT 0.29
Grain 0.13
MAP 0.11
-1.0 -0.5 0.0 0.5 1.0 1.5
Parameter estimate
Fixed effect
Fixed effect

Figure 4

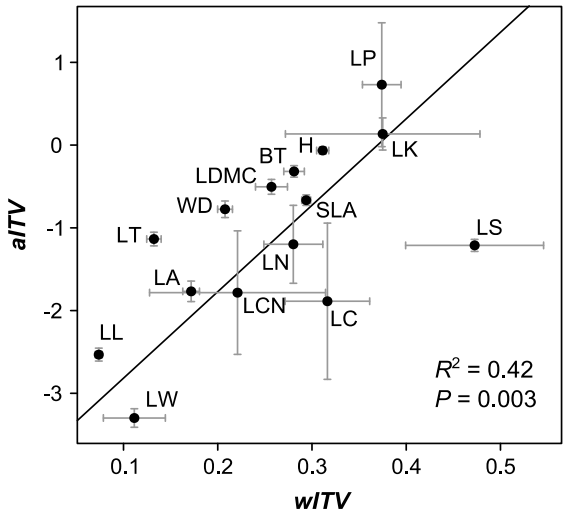
LP
H
LK
BT
LDMC
WD
SLA
LT
LS
LN
LA
LCN
LC
LL
LW
R^2 = 0.42
P = 0.003
1
0
-1
-2
-3
0.1
0.2
0.3
0.4
0.5
alTV
wlTV

Figure 5

Box 1: Trait variance partitioning

Within-community

For each community *i* and each functional trait within a given study, we calculated the abundance-weighted interspecific and intraspecific trait variance, which sum to the total within-community trait variance (de Bello *et al.* 2011). We calculated the relative contribution of ITV to within-community trait variance (*wITV*) of each community as the ratio of the intraspecific trait variance over the total within-community trait variance:

$$wITV_i = 100 \times \frac{\sum_j p_{ij} \times \frac{1}{N_{ij}} \sum_k (t_{ijk} - t_{ij})^2}{\sum_j p_{ij} \times \left(t_{ij} - \sum_j p_{ij} t_{ij} \right)^2 + \sum_j p_{ij} \times \frac{1}{N_{ij}} \sum_k (t_{ijk} - t_{ij})^2},$$

where p_{ij} is the relative abundance of species *j* in community *i*, N_{ij} and t_{ij} are the number of sampled individuals and the mean trait value, respectively, of species *j* in community *i*, and t_{ijk} is the trait value of individual *k* in community *i* belonging to species *j*. The relative amount of intraspecific trait variation within communities in each study was then calculated by averaging $wITV_i$ over the communities.

Among-community

The relative contribution of intraspecific variability to among-community trait variance (*aITV*) was calculated in several steps. For each study, the weighted mean of each trait in each community *i* was computed using the community-level species mean trait value (CWM_i) and the study-level species mean trait value ($CWMfixed_i$). The intraspecific variability effect was measured as $CWMintra_i = CWM_i - CMWfixed_i$. The sum of squares associated with CWM_i, $CWMintra_i$ and $CMWfixed_i$ across communities (SStot, SSintra and SSfixed) was calculated using an intercept-only linear model. SStot represents the total among-community trait variation,

SSintra represents variation due exclusively to intraspecific variability, and SSfixed represents variation due exclusively to changes in species occurrence and relative abundance (i.e., species turnover). We then calculated *aITV* as:

$$aITV = \ln(\frac{SS_{intra}}{SS_{fixed}}).$$

This provides a symmetric measure of the relative contributions of ITV and species turnover to the total among-community trait variation, with positive values indicating a larger effect of ITV and negative values indicating a larger effect of species turnover. We chose to measure ITV relative to species turnover rather than relative to the total among-community variation because in some cases, the ITV and species turnover effects oppose each other, potentially resulting in the total among-community variation approaching zero. The covariation between the effects of intraspecific variability and species turnover was calculated as:

$$\mathrm{cov} = 100 \times \frac{SS_{tot} - SS_{intra} - SS_{fixed}}{SS_{tot}}.$$